

A New Subspecies of the Agamid Lizard, *Japalura polygonata* (Hallowell, 1861) (Reptilia: Squamata), from Yonagunijima Island of the Yaeyama Group, Ryukyu Archipelago

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Abstract: *Japalura polygonata*, occurring in the East Asian islands, is currently divided into three subspecies—*J. p. polygonata* from the Amami and Okinawa Groups of the central Ryukyus, *J. p. ishigakiensis* from the Miyako and Yaeyama Groups of the southern Ryukyus, and *J. p. xanthostoma* from northern Taiwan. A new subspecies is described for this species from Yonagunijima Island of the Yaeyama Group. This subspecies differs from other conspecific subspecies in having distinctly enlarged and irregularly arranged scales on the dorsolateral surface of the body. In other subspecies, the degree of enlargement of such scales is smaller, and they usually form somewhat regular rows in a transverse direction on the flanks, and in a longitudinal direction in the paravertebral region. Males of the present subspecies differ from those of other subspecies in having a series of large white spots against a dark grayish tan on the dorsolateral surface of the body, whereas the females are characterized by brilliant green dorsal coloration.

Key words: *Japalura polygonata*; New subspecies; Reptilia; Geographic variation; Yonagunijima Island; Ryukyu Archipelago

INTRODUCTION

The agamid genus *Japalura* consists of 24 species and two subspecies distributed from northern India and Nepal to the East Asian islands (Ota, 2000a,b; Gau and Hou, 2002; but see Marcey et al., [2000] for the possible non-monophyly of the western and eastern components, and Schleich and Kästle [2002] for a different generic arrangement). Of the species of *Japalura*, *J. polygonata* occupies the northeasternmost extremity of the geo-

graphic range of the genus (and actually of the family Agamidae as well), being distributed in northern Taiwan and most islands of the Ryukyus south of the Tokara Group. Three subspecies are currently recognized for the species—*J. p. polygonata* from the Amami and Okinawa Groups of the central Ryukyus, *J. p. ishigakiensis* from the Miyako and Yaeyama Groups of the southern Ryukyus, and *J. p. xanthostoma* from northern Taiwan (Ota, 1991). In the process of their infraspecific classification, however, very few island samples have been examined. Hallowell (1861), for example, described the species (as *Diploderma polygonatum*) only on the basis

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of a single specimen from "Amakarima Island" (subsequently restricted to the Kerama Islands of the Okinawa Group by Stejneger [1907]). Van Denburgh (1912), in describing two subspecies, *J. p. ishigakiensis* and *J. p. miyakensis*, examined specimens only from Ishigakijima and Iriomotejima Islands for *ishigakiensis*, Miyakojima Island for *miyakensis*, and Okinawajima and Amamioshima Islands for the nominotypical subspecies. Although several subsequent authors referred to populations of *J. polygonata* on some other islands (e.g., Okada, 1937; Nakamura and Uéno, 1963; Ikehara et al., 1984; Toyama, 1985), or proposed infraspecific classification different from that proposed by Van Denburgh (1912) (Nakamura and Uéno, 1963; Matsu-moto, 1979; Ota, 1991), none of them investigated between-island variation in *Japalura polygonata* in detail.

Yonagunijima Island (Fig. 1), a component

of the Yaeyama Group, is the westernmost island of the Ryukyus. Its herpetofauna, while sharing most species and subspecies exclusively with other southern Ryukyu islands (Yasukawa et al., 1996; Toda et al., 1997; Ota, 1998, 2000c; Chen et al., 2001), includes two endemic snakes (*Calamaria pavimentata miyarae* and *Elaphe carinata yonaguniensis*), whose closest relatives occur only in Taiwan and the southern part of the continent (Takara, 1962; Ota, 1998, 2000c). The occurrence of *Japalura polygonata* on Yonagunijim Island was first noted in Okada's (1937) monograph on the basis of information from "KURODA". Curiously enough, however, Okada (1937), while introducing Van Denburgh's (1912) subspecific classification of *J. polygonata*, retained the Yonagunijima population in the nominotypical subspecies (p. 93). Nakamura and Uéno (1963) also assigned the Yonagunijima population to *J. p. polygonata*

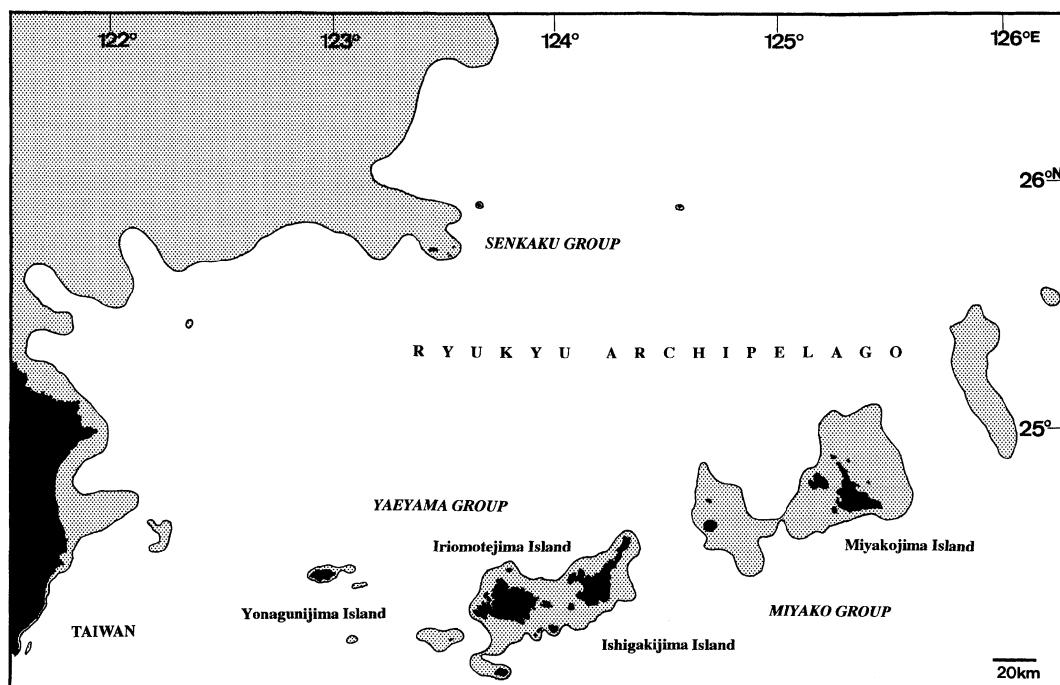


FIG. 1. Map of the southern Ryukyus and adjacent regions showing the location of Yonagunijima Island, the type locality of *Japalura polygonata donan* subsp. nov. The stippled portions denote current sea areas that are considered to have constituted additional lands during the Late Pleistocene (i.e., sea areas shallower than 120 m: Ota et al., 1993).

together with all other Ryukyu populations under the assumption that *Japalura swinhonis* Günther, 1864 (including *J. mitsukurii* Stejneger, 1898: see Ota, 1991) of Taiwan should be regarded as a subspecies of *J. polygonata*, a view clearly negated on the basis of recent morphological and ecological observations by Ota (1988a, 1991). Matsumoto (1979), on the other hand, implicitly synonymized Van Denburgh's (1912) *J. p. miyakensis* with *J. p. ishigakiensis*, because he referred to all Yaeyama (including Yonagunijima Island) and Miyako populations as *J. p. ishigakiensis*.

Recently I had a chance to examine a good series of *Japalura* specimens from Yonagunijima Island for the first time. Comparison of these specimens with specimens of *J. polygonata* from many other islands of the Ryukyus and Taiwan revealed the presence of slight but consistent differences between the Yonagunijima specimens and the remainder. However, they exclusively shared an orange [males] or yellow [females] spot at the center of the gular. Because such a gular spot was not observed in other species so far studied (Ota, 1991), I tentatively regard this spot as synapomorphy of *J. polygonata*, and thus describe the Yonagunijima population as a new subspecies of this taxon.

MATERIALS AND METHODS

A total of 56 specimens (42 adult males, 11 adult females, and three juveniles) collected from Yonagunijima Island were compared with 354 specimens of *J. p. polygonata* from eight islands of the central Ryukyus, 177 specimens of *J. p. ishigakiensis* from three islands of the southern Ryukyus, and 148 specimens of *J. p. xanthostoma* from four localities in northern Taiwan (see Appendix for further details). Of the 56 Yonagunijima specimens, two males and two females were also subjected to karyotyping following Ota (1988b).

Morphological characters were examined following Ota (1991). Sexual difference in adult snout-vent length (SVL) was examined by t-test, and was also expressed by the sexual

dimorphism index (SDI) proposed by Gibbons and Lovich (1990) as:

$+x/y$, when $x > y$; or $-y/x$, when $x < y$
where x and y denote means for adult females and adult males, respectively. Differences in meristic characters among samples were tested for statistical significance by Kruskal-Wallis test and Dunn's multiple comparison test following Zar (1984).

In the following sections, catalogue numbers of specimens deposited in the Zoological Collection of the Kyoto University Museum, and Masami Hinoue's private collection are preceded by KUZ and HPN, respectively. The other institutional acronyms follow Leviton et al. (1985).

Japalura polygonata donan subsp. nov.

Fig. 2

Japarula [sic] *polygonata polygonata*: Okada, 1937:93 (part).

Japalura polygonata polygonata: Nakamura and Uéno, 1963:103 (part).

Japalura polygonata ishigakiensis: Matsumoto, 1979:17 (part); Ota, 1983:16 (part); Toyama, 1985:63 (part); Ikehara et al., 1994: 275 (part); Ota, 1991:288 (part).

Holotype

KUZ R234, an adult male collected at Mt. Urabudake ($24^{\circ}27'N$, $123^{\circ}00'E$, alt. 130 m), Yonagunijima Island, on 17 August 1981 by H. Ota.

Paratypes

KUZ R102, an adult female collected at Higawa, Yonagunijima Island, on 30 March 1981 by H. Ota; KUZ R231, 238, two adult females, sampling data same as the holotype; KUZ R415, an adult female collected between Higawa and Arakawabana, Yonagunijima Island, on 7 March 1982 by H. Ota; KUZ R971, 972, 975, 979, 997, four adult males and one adult female collected between Mt Urabudake and Sonai, Yonagunijima Island, on 26 March 1983 by T. Hayashi, K. Kawamura, S. Kobayashi, A. Mori, and H.

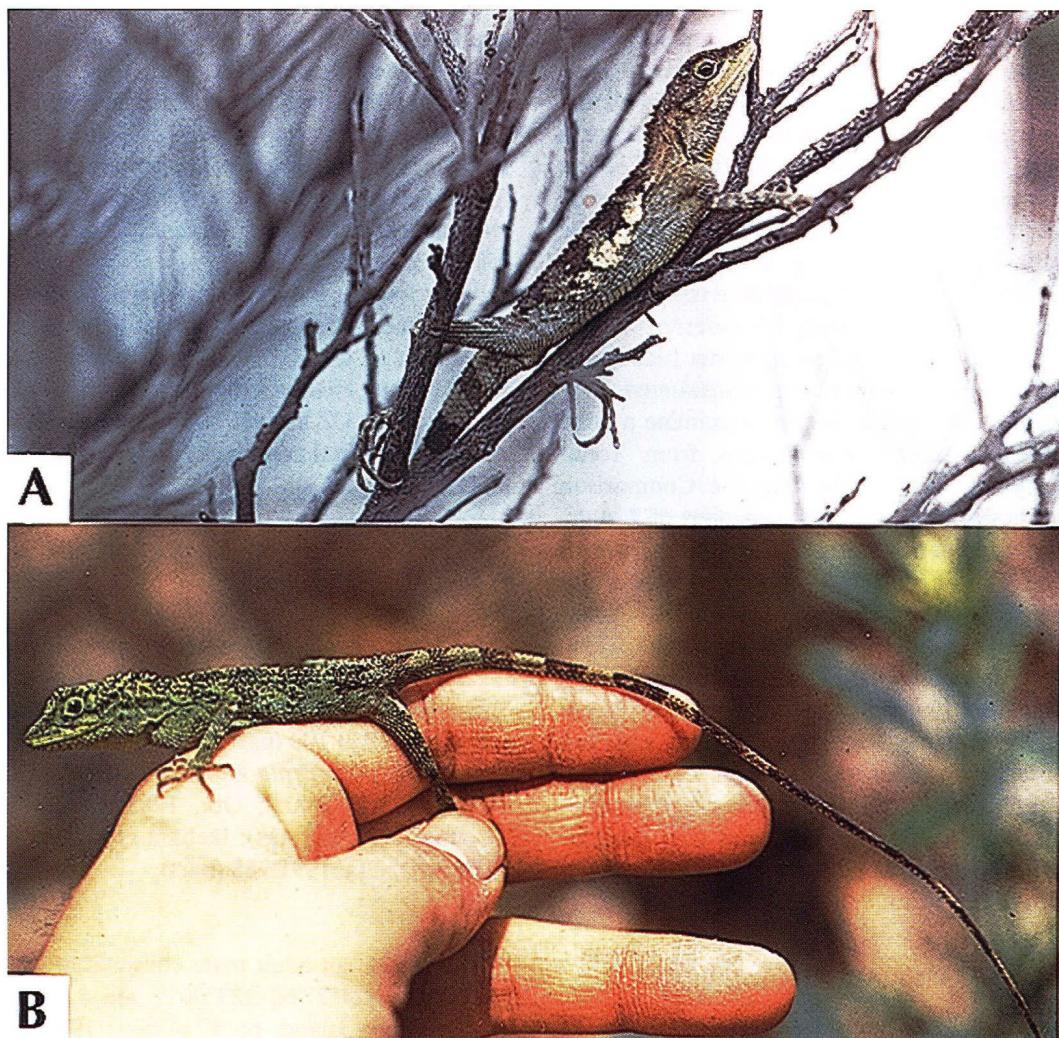


FIG. 2. Male paratype (A. KUZ R3294) and female paratype (B. KUZ R4515) of *Japalura polygonata donan* subsp. nov.

Ota; KUZ R1382, 1420, two adult females collected at Kubura, Yonagunijima Island, on 27 July 1983 by H. Ota; KUZ R2000–2003, 2164, 2876, 3261–3263, 3265, 3269, 3270, 3281–3283, 3289, 3291–3294, 3982, 4515, 4517, 4518, 22 adult males, two adult females, and three juveniles collected at Mt. Urabudake on 15 July 1984 by H. Ota; KUZ R28117, 28118, two adult females collected at Kubura on 25 June 1993 by H. Ota; 56152–56156, 56158–56167, 15 adult males collected at Mt. Urabudake on 25 March 2003 by H. Ota.

Diagnosis

Adult females largest among the subspecies of *J. polygonata* (55.5–70.5 mm in snout-vent length [SVL] [$\bar{x}=63.3$]), brilliant green dorsally. Adult males almost as large as females (57.7–71.0 mm SVL [$\bar{x}=65.6$]), with a series of large white spots against dark grayish tan on the lateral surface of body. Middorsal scales 30–44 ($\bar{x}=37.1$), fewer than those in other subspecies, but with some range overlaps (34–47 [$\bar{x}=40.8$] in *J. p. polygonata*; 35–53 [$\bar{x}=44.3$] in *J. p. ishigakiensis*, and 37–48

[$\bar{x}=42.4$] in *J. p. xanthostoma*); some dorsolateral body scales distinctly enlarged, irregularly arranged; orange (male) or yellow (female) spot at center of gular in adults; sexual size dimorphisms not evident; buccal and palatal mucosa light pinkish gray.

Etymology

The subspecific epithet, “*donan*”, refers to an old vernacular name of Yonagunijima Island. “*Donan*” is not in official use at present. However, this term is still commonly used by the inhabitants of this island. “*Donan*” also refers to a kind of special liquor of Yonagunijima, which added a great joy to my fieldwork there.

Description of holotype

Measurements (in mm): SVL 69.4; head length 21.8; snout-eye length 9.0; interorbital distance 10.9; fore-limb length 33.6; axilla to groin distance 31.8; hindlimb length 55.4; tibia length 18.1; toe IV length 13.4; tail length 178.1.

Snout tapering, roundish at tip; rostral quadrangular, about three and a half times as wide as long, covering anterior tip of snout; seven scales, in contact with rostral; nasal separated from rostral by one scale, contacted by this intervening scale, first supralabial, and six other scales; supralabials not keeled, seven on left, six on right, second separated from nasal by one scale; a longitudinal row of keeled and moderately enlarged scales, each larger than half the size of supralabials, behind nasal to imaginary vertical line from posterior margin of eye; one row of much smaller scales intervening between preceding row and supralabials; mental pentagonal, surrounded by four scales; infralabials slightly keeled, seven on both sides; a row of enlarged scales on anterior part of lateroventral corner of mandible, first ones on both sides and second one on right side contacting first infralabials, the others separated from labial series by one or two scales; tympanum completely concealed beneath skin; dorsal and lateral surfaces of head covered with enlarged and

irregularly arranged scales, each with a distinct midline keel; some scales in occipital region with a few additional weak keels, making surface rugose; interparietal surrounded by eight scales; superciliaries imbricate, each overlapping one third to half with successor; scales around eye very small; scales on ventral surface of head obliquely arranged, most of them more or less keeled medially; but a few not keeled; longitudinal gular fold very slight; slender, hair-like sense organs present on several head scales; longitudinal middorsal scale row consisting of 40 enlarged, strongly keeled scales, anterior eight especially enlarged, and much compressed, each almost as broad as high, forming a nuchal crest; scales adjacent to middorsal row smaller, directed backward and slightly upward; most scales in dorsolateral and lateral regions of body weakly keeled, as large as or smaller than those on venter, intermixed with much enlarged, strongly keeled, irregularly arranged scales; scales on ventral surfaces of body and limbs moderately keeled and regularly arranged longitudinally; slight oblique fold on each shoulder; limbs relatively short, toe IV (exclusive of claw) reaching to middle of eye when hindlimb adpressed forward; scales on dorsal surface of limb larger than those on ventral surface; finger and toe I shortest, finger IV almost as long as finger III, toe IV distinctly longer than toe III; subdigital scales 9–9, 13–13, 18–19, 19–19, 12–12 on left-right fingers I, II, III, IV, Y, 8–7, 13–13, 20–20, 23–25, 16–16 on left-right toes I, II, III, IV, V; tail slightly compressed, oval in cross section, with slightly enlarged median scales on dorsum; subcaudal scales strongly keeled, distinctly larger than scales on dorsum.

Color in life

Dorsal ground color dark grayish tan; infraorbital region paler than surroundings but not white; otherwise, no distinct markings on head; each side of body with five quadrangular white spots forming a longitudinal row; second and third spots partially fused on left side, separated on right side; ground color of limbs and tail slightly lighter than that of trunk,

several indistinct dark annuli on limbs, 15 dark annuli on tail.

Ventral surface of head light gray, without markings except for one large orange spot in midst of gular region; ventral surfaces of remaining part of body pale gray. Buccal-palatal mucosa light pinkish gray.

Color in ethanol

Dorsal ground color turned slightly paler; the orange spot on gular faded to invisible; the remaining color patterns similar to those in life.

Variation

Variations in some meristic characters and SVL are given in Tables 1 and 2, respectively. There are no significant differences in those meristic characters between the sexes ($P>0.05$). Unlike in *J. p. polygonata* and *J. p. ishigakiensis* where sexual size dimorphism is evident with males being larger, *J. p. donan*, as well as *J. p. xanthostoma*, does not show significant differences in adult SVL between sexes (Table 2).

Live coloration of females remarkably differs from that of males. Dorsal surface of

TABLE 1. Variation in meristic characters ($\bar{x} \pm SD$, followed by ranges in parentheses) among island samples of *Japalura polygonata* examined. Abbreviations are: SER, number of scales contacting rostral; IOS, number of scales touching an imaginary line drawn between outer edges of left and right supraciliaries; DC, middorsal crest-like scales from just posterior to occipital granules to just above anterior margin of vent; T4S, slightly enlarged scales beneath toe IV, counted from branching point with toe III to base of claw.

Subsp.	Island	n	SER	IOS	DC	T4S	
<i>polygonata</i>	Kikajima	34	8.31±0.82 (7–9)	12.46±1.28 (10–15)	39.77±2.12 (36–44)	25.54±1.28 (23–27)	
	Amamioshima	17	8.61±0.70 (7–10)	12.87±1.10 (11–15)	41.23±2.50 (37–45)	25.55±1.27 (23–28)	
	Kakeromajima	33	8.55±0.74 (7–10)	12.58±1.16 (11–15)	40.12±2.53 (36–45)	25.76±1.32 (23–28)	
	Tokunoshima	53	8.52±0.78 (7–10)	12.26±1.30 (10–15)	41.32±2.78 (35–45)	25.52±1.18 (23–27)	
	Iheyajima	28	8.65±0.70 (7–10)	12.02±0.99 (11–15)	41.16±2.42 (36–44)	25.30±1.24 (23–27)	
	Okinawajima	61	8.29±0.98 (6–10)	11.95±1.16 (10–14)	40.72±3.06 (33–49)	26.05±1.31 (23–29)	
	Tokashikijima	63	8.03±0.85 (7–9)	12.13±1.17 (9–14)	39.44±2.40 (35–43)	25.50±1.68 (23–30)	
	Kumejima	65	8.25±0.82 (6–10)	12.04±1.22 (10–15)	40.04±2.84 (34–44)	25.84±1.47 (23–28)	
	<i>ishigakiensis</i>	Miyakojima	41	8.01±1.02 (5–11)	13.22±1.19 (11–16)	44.80±3.27 (39–52)	23.52±1.23 (21–26)
		Ishigakijima	80	8.40±0.87 (6–10)	12.41±1.17 (11–15)	45.62±2.51 (39–52)	22.99±1.50 (20–27)
		Iriomotejima	56	7.78±1.08 (6–10)	12.91±0.97 (10–15)	44.04±2.85 (37–52)	23.25±1.40 (19–26)
<i>donan</i>	Yonagunijima	53	7.31±0.56 (7–9)	11.74±1.16 (10–14)	37.17±2.68 (30–44)	22.82±1.23 (20–27)	
<i>xanthostoma</i>	Taiwan	148	8.06±0.94 (5–10)	13.15±0.90 (11–15)	44.39±3.43 (38–55)	23.55±1.59 (20–29)	

TABLE 2. Variation in adult male and female SVLs (mm) in island samples of *Japalura polygonata* examined. Significance levels of difference in adult SVL between sexes from the same islands are as follows: +++, $P < 0.001$; ++, $P < 0.01$; -, $P > 0.05$. SDI, sexual dimorphism index (Gibbons and Lovich, 1990; see text).

Subsp.	Island	Sex	n	\bar{x}	SD	Range	SDI
<i>polygonata</i>	Kikaijima+++	male	27	67.6	5.8	55.1–79.2	-1.164
		female	7	58.1	5.2	51.5–68.8	
	Amamioshima++	male	7	68.9	6.1	54.0–80.0	-1.164
		female	10	59.2	5.0	51.0–69.5	
	Kakeromajima++	male	21	68.0	6.0	54.3–79.0	-1.174
		female	11	57.9	4.8	51.8–69.0	
	Tokunoshima++	male	42	69.1	6.3	54.2–80.5	-1.161
		female	11	59.5	5.4	53.9–69.2	
	Iheyajima++	male	18	68.1	5.8	53.0–77.6	-1.178
		female	10	57.8	4.3	50.8–68.2	
<i>ishigakiensis</i>	Okinawajima++	male	55	67.1	6.6	54.0–80.2	-1.128
		female	33	59.5	3.9	52.5–68.5	
	Tokashikijima++	male	34	67.3	5.4	53.8–76.9	-1.152
		female	28	58.4	4.1	53.1–67.9	
	Kumejima++	male	40	67.4	6.2	54.2–80.0	-1.164
		female	22	57.9	5.1	52.1–68.2	
	Miyakojima++	male	22	62.2	6.9	47.5–72.0	-1.150
		female	12	54.1	3.6	51.0–62.0	
	Ishigakijima++	male	56	59.9	3.2	52.9–66.0	-1.093
		female	24	54.8	3.8	48.0–61.0	
<i>donan</i>	Iriomotejima++	male	37	59.4	3.7	48.5–67.0	-1.094
		female	15	54.3	3.5	47.0–60.5	
	Yonagunijima-	male	42	65.6	2.7	57.7–71.0	-1.036
		female	11	63.3	4.4	55.5–70.5	
<i>xanthostoma</i>	Taiwan-	male	112	60.8	2.9	50.3–68.0	-1.020
		female	37	59.6	3.2	51.7–65.9	

body of females is brilliant green, with no white spots but with several obscure dark cross bands around the middorsal region. In females, there is a somewhat obscure yellow spot in midst of gular region.

Karyotype

Like other subspecies of *J. polygonata* (Ota, 1991), *J. p. donan* has a karyotype consisting of $2N=46$ uniaxed chromosomes in a graded series.

Distribution and habitat

Japalura polygonata donan is endemic to Yonagunijima Island of the Yaeyama Group, Ryukyu Archipelago, Japan. Most specimens were found in the marginal portions of well-recovered secondary forests consisting of evergreen broad-leaf trees.

Ecological notes

All three females collected in March had ovarian follicles (3–5 mm in diameter) only, whereas the six females collected between mid July and mid August exhibited flaccid, empty

oviducts and poorly developed ovarian follicles (<3 mm in diameter). Of the remaining two females, both collected in the late June, one had two and one large follicles (7 mm in diameter) in left and right ovaries, respectively. The other had one elliptic egg (15.8×7.5 mm) in each oviduct. It is thus probable that in this subspecies ovulation and oviposition occur chiefly in late June or early July.

One colubrid snake, *Dinodon rufozonatum walli*, collected at Mt. Urabudake in August 1981, had two slightly digested adult male *J. p. donan* in its stomach.

DISCUSSION

Japalura polygonata donan shares an orange (males) or yellow (females) spot in the center of the gular exclusively with the other conspecific subspecies. However, it differs from the latter in having distinctly enlarged and irregularly arranged scales on the dorsolateral surface of the body. In other subspecies, the degree of enlargement of such scales is smaller, and they usually form somewhat regular rows in a transverse direction on the flanks, and in a longitudinal direction in the paravertebral region. In the present subspecies, the middorsal scales, ranging from 30 to 44 ($\bar{x}=37.1$), are fewer than in other subspecies, although there are some range overlaps (34–47 [$\bar{x}=40.8$] in *J. p. polygonata*; 35–53 [$\bar{x}=44.3$] in *J. p. ishigakiensis*, and 37–48

[$\bar{x}=42.4$] in *J. p. xanthostoma*: Tables 1 and 3). The males of *J. p. donan* differs from the males of other subspecies in having a series of large white spots against dark grayish tan on the dorsolateral surface of the body. In other subspecies, the dorsolateral surface of the body has a continuous white or yellow band instead. The adult females of *J. p. donan* are the largest among the females of *J. polygonata* populations (55.5–70.5 mm in SVL, [$\bar{x}=63.3$ mm]), and are almost as large as the adult males of the same subspecies (57.7–71.0 mm SVL [$\bar{x}=65.6$]). Thus, the male large sexual size dimorphism is not evident in this subspecies unlike in other subspecies exclusive of *J. s. xanthostoma* (Table 2). The females *J. p. donan* are also characterized by the brilliant green coloration on the dorsum of the body. The buccal and palatal mucosa of the present subspecies is not yellowish as in *J. p. xanthostoma*.

Taxonomic treatment of allopatric, slightly but diagnosably diverged entities like the Yonagunijima population of *J. polygonata* is a matter of serious debate among taxonomists, depending on which school they belong to (Frost and Hillis, 1990; Grismer et al., 1994). In the present case, the population is clearly diagnosable (see above). Moreover, from the geographic pattern of variation in *J. polygonata* as a whole (Table 3), naming of the Yonagunijima population is not an arbitrary slicing of a geographically clinal entity, a

TABLE 3. Comparisons of island samples of *Japalura polygonata* by Kruskal-Wallis test (KWT) and Dunn's multiple comparison test. Abbreviations of island samples are: KK, Kikajima; AO, Amamioshima; KR, Kakeromajima; TN, Tokunoshima; IH, Iheyajima, OK, Okinawajima; TK, Tokashikijima; KM, Kumejima; MY, Miyakojima; IS, Ishigakijima; IR, Iriomotejima; YN, Yonagunijima; TW, Taiwan. See Table 1 for character abbreviations. Significance levels for KWT are: +++, P<0.001; +, P<0.05. Samples sharing same superscript letters showed no significant differences in Dunn's multiple comparison test (P>0.05).

Characters KWT		Descending order of samples													
SER	+++	IH ^a	AO ^a	KR ^{ab}	TN ^{ab}	IS ^{bc}	KK ^{bc}	OK ^c	KM ^c	TW ^d	TK ^d	MY ^{de}	IR ^e	YN ^e	
IOS	+	MY ^a	TW ^a	IR ^{ab}	AO ^{bc}	KR ^{abc}	KK ^{bc}	IS ^{bcd}	TN ^{bcd}	TK ^{cd}	KM ^{cd}	IH ^{cd}	OK ^{de}	YN ^e	
DC	+++	IS ^a	MY ^{ab}	TW ^{ab}	IR ^b	TN ^c	AO ^c	IH ^{cd}	OK ^{cd}	KR ^{cd}	KM ^d	KK ^d	TK ^d	YN ^e	
T4S	+++	OK ^a	KM ^a	KR ^a	AO ^a	KK ^a	TN ^a	TK ^a	IH ^a	TW ^b	MY ^{bc}	IR ^{bcd}	IS ^{cd}	YN ^d	

practice that can not be justified by the standards of modern taxonomy (e.g., Frost and Hillis, 1990). Also, one may argue that the Yonagunijima population deserves the status of a full species rather than a subspecies of *J. polygonata*. However, the presence of less diverged populations on both sides of Yonagunijima Island that are currently treated as two conspecific subspecies (i.e., *J. p. ishigakiensis* of the remaining Yaeyama Group and Miyako Group islands, and *J. p. xanthostoma* from Taiwan; Ota, 1991) makes it safer at present to retain the Yonagunijima population also at the subspecific status. Future detailed investigations of historical relationships at the population level and captive hybridization experiments may lead to elevation of *J. p. donan* to the full species status.

Yonagunijima Island is separated from other neighboring islands and the continent by straits deeper than 500 m (Maritime Safety Agency, 1978: Fig. 1). This suggests that the island has been isolated for a long period of time (e.g., Ota et al., 1993). *Japalura polygonata donan* and the two other reptiles endemic to Yonagunijima Island (i.e., *Calamaria pavimentata miyakai* and *Elaphe carinata yonaguniensis*) are likely to have diverged from their relatives in Taiwan and the southern Ryukyus through such an isolation.

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APPENDIX

Comparative specimens examined

Japalura polygonata polygonata. Ryukyu Archipelago: Okinawa Group: Kerama Islands (type loc.): Tokashikijima Is.: KUZ R2300–2306, 2360–2369, 4082, 4085, 4087–4101, 4494–4514, 4568, 4569, 4574–4576, OPM H0187, 0188, 0437; Okinawa Group, Kumejima Is.: KUZ R2241, 2333, 2334, 2421–2424, 4077, 4444–4493, 4578–4582, OPM H0082, 0451; Okinawa Group: Okinawajima Island: AMNH 21167–21169, 21172, HPN 42, 51, 55, 56, 59, 60, 69–71, 88–91, 383, 439, KUZ R1146–1200, 1355–1358, 1380, 1381, 1383–1385, 1423, 1483, 1485, OMNH R93–98, 733, 734, 736, 737, 744, 759–762, 897, 898, 1393, 1394, 1451–1453, 1455–1458, 1460, 1618, 1704); Okinawa Group: Iheyajima Is.: KUZ R2267, 2307; 2308, 2370–2378, 3950–3958, 4083, 4086; 4570–4573, OPM HJ0029; Ryukyu Archipelago: Amami Group: Tokunoshima Is.: KUZ R2159–2162, 2425–2429, 2940, 2943–2945, 3000, 3014, 3057, 3102, 3224, 3225, 3286, 3457, 3465, 3965, 4003–4031, 4033; Amami Group: Kakeromajima Is.: KUZ R2396–2408, 3984–3999, 4063–4066; Amami Group: Amaioshima Is.: KUZ R2163, 2379–2389, 2968–2971, OPM H0028; Amami Group: Kikajima Is.: KUZ R2266, 2321, 2335, 2337,

2338, 2393–2395, 2409–2420, 3962, 4059–4062, 4067–4076.

J. p. ishigakiensis. Ryukyu Archipelago: Yaeyama Group: Ishigakijima Is. (type loc.): KUZ R3–5, 225, 227, 702–714, 719–722, 903, 905, 906, 934–936, 1023, 1373–1379, 1386, 1474–1480, 2008, 2205–2207, 2218, 2219, 2222–2224, 2226, 2877, 2878, 2880–2883, 2885, 2897, 2928, 3052, 3279, 3280, 3290, 3977, 4519. OMNH R772, 786, 787, 1653, 1696–1699, OPM H0054, 0093; Yeyama Group: Iriomotejima Is.: KUZ R2196–2204, 2356–2359, 2390–2392, 3274, 3275, 3947, 3948, 3959–3961, 3978, 3979, 4102, 4103, 4365, 4366, 4521, 4522, 4524–4537, 4540, OPM H0025, 0051, 0052, 0074, 0081, 0085, 0183–0186; Ryukyu Archipelago: Miyako Group: Miyakojima Is. (type loc. of *J. p. miyakensis*): KUZ R2150–2158, 2183, 2339–2348, 4080, 20 uncatalogued specimens.

J. p. xanthostoma. Taiwan: Taipei: Waishuangchi (type loc.): KUZ R9855 (holotype), KUZ R1600–1602, 1609, 1610, 1649, 1657, 2058, 2059, 2715, 2809, 2919–2923, 2933, 2978, 2979, 3036, 3056, 3219, 3964, 4360, 4361, 6707–6710, 7519–7534, 7537–7545, 7846, 7851–7855, 7861–7871, 7880–7882, 7884, 7901, 7922, 7941, 7942, 7952, 7961, 7973, 7991, 7992, 8009, 8010, 8019, 8020, 8066, 8067, 8099, 8420, 8446–8452, 9775–9780, 9842–9854, 9856–9861, 13010–13019; Taipei: Tansui: KUZ R8424–8431; Taipei: Peitou: AMNH 77093; Taiwan: Ilan: Tungao: KUZ R6914, 6915, 6943, 6944, 6947 (all paratypes).

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